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The evolution of animal societies

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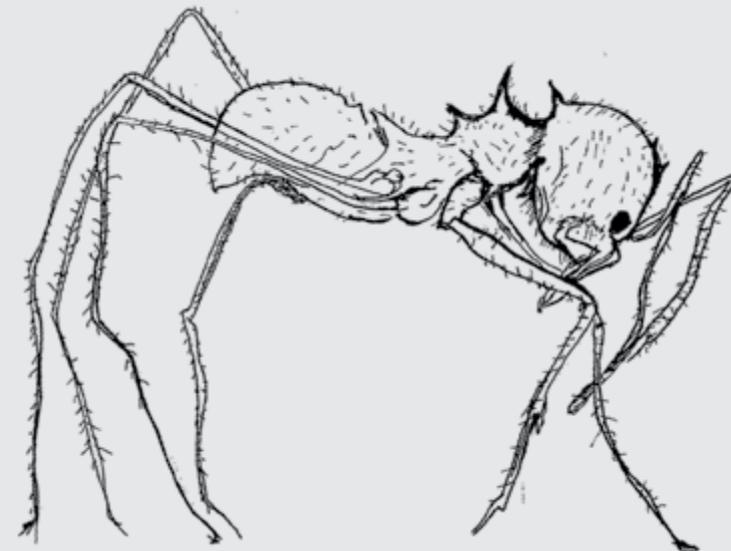
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AFTERTHOUGHTS:
THE EVOLUTIONARY TRANSITION TO
EUSOCIALITY



John Maynard-Smith and Eörs Szathmáry (1998) defined major evolutionary transitions in their seminal book with the same title as follows: *The Major Transitions in Evolution* are events in the history of life that opened unprecedented avenues of biological novelty. Maynard-Smith and Szathmáry were concerned with how evolution always seems to reach new levels of complexity. They argued micro-evolutionary processes do not necessarily lead to an ever increasing level of complexity. Instead, they speculated that throughout the history of life, biological complexity increased by exploring the paths of novelty left open by eight major events, the major evolutionary transitions. Besides defining the eight major transitions, Maynard-Smith and Szathmáry outlined three features that characterize many, but not all, the transitions: 1) entities from a lower organizational level lose their capacity to reproduce independently; 2) entities develop division of labour, and 3) there are changes in the processes of information storage and transmission. The first of those features includes the problem of the evolution of cooperation. In order to achieve a new organizational unit composed of entities at a lower level, the lower entities must forgo their selfish reproductive interests and cooperate to form a new unit. The evolution of eusociality was classified by Maynard-Smith and Szathmáry as one of the major transitions. The evolution of eusociality, arguably, has the three features of major transitions mentioned above, given that: 1) individual animals can no longer reproduce independently after they are part of a eusocial colony; 2) there is division of labour, with castes specialized on different tasks, and 3) the organization of a colony requires new paths of information transfer between individuals.

Even before the major transition paradigm the evolution of eusociality had been a major topic of interest for evolutionary biologists. The cornerstone of eusociality, reproductive division of labour, has been seen as the pinnacle in social evolution, where some individuals reach a level of commitment to the social enterprise that they forgo their own reproduction (i.e. the worker trait). Formal theories of the evolution of eusociality have focused mainly -if not only- on explaining when and how natural selection would favour individuals to become altruistic workers (Hamilton 1964*b*; Trivers and Hare 1976; Crozier 2008; Nowak et al. 2010; Fromhage and Kokko 2011; Gardner et al. 2012; Alpedrinha et al. 2014, 2014; Avila and Fromhage 2015; Olejarz et al. 2015). The exclusive focus on the conditions for natural selection to favour the altruistic trait means that the theories of eusociality are ignoring developmental

aspects such as: the origin of the worker trait, and the mechanisms of division of labour inside a colony (West-Eberhard 2003; Hunt 2012). Hence, these theories are incomplete, and could be referred to as *selective* rather than *evolutionary* theories of eusociality (Frank 1998; Uller and Helanterä 2014). In the chapters 3 and 4 of this thesis we followed this tradition and present a series of evolutionary models to understand when and how natural selection favours the establishment of eusocial colonies with individuals that forgo their own reproduction. In chapter 3 we focus on a series of models that integrate a set of traits (preadaptations) that had been proposed to favour the evolution of the worker trait. Furthermore, we considered the co-evolution of the sex ratio strategy of females in two different broods together with the worker trait. The model unveiled an evolutionary feedback between the sex ratio strategy and the worker trait, where the evolution of worker behaviour is facilitated by certain sex ratio biases, and once worker behaviour is present changes selection on the sex ratio strategy. In chapter 4, we extended one of the life history structures modelled in chapter 3 and considered the effect of the queen-worker conflict over sex ratio in the evolution of the worker trait. Specifically, we allowed the evolution of worker fratricide as a mechanism to influence the sex ratio of the colony, as well as different sex ratio strategies for solitary and social nests.

The evolution of eusociality is, however, more than just selection of the worker trait. The functioning of a eusocial colony requires close communication between the colony members. The gathering and use of resources is coordinated by the members of the different castes of a colony. Besides, in order for the colony to adaptively tune the allocation of individuals of different castes, the expression of the worker trait itself must be determined by either environmental or social factors. A full theory of the transition from solitary to eusocial life must include all these complexities. In this afterthoughts section, I will discuss how the models presented here can be a stepping stone towards a more complete evolutionary theory of eusociality.

Towards an evolutionary developmental theory of eusociality

Evolutionary biology has traditionally ignored and neglected the role of development and mechanisms in the explanations of morphology and behaviour (West-Eberhard 2003). However, in recent years evolutionary biologists seem to be more interested and aware of the relevance of development in evolutionary processes (Laland et

al. 2011*b*), particularly in the origin of new phenotypes (Badyaev 2011). Social evolution has not been the exception to this pattern (West-Eberhard 1987*b*; Uller and Helanterä 2014). Traditional formal models of the evolution of social behaviours have investigated the action of natural selection in changing allele frequencies, when those alleles are the direct and unique cause of social behaviours (Hamilton 1964*a*; Frank 1998; Gardner et al. 2011). Focusing on the effects of selection only amounts to ignoring the proximate causes behind those behaviours (Laland et al. 2011*b*). Ignoring proximate causes, however, is not due to theoreticians' ignorance but rather a simplification made to facilitate the understanding of the action of natural selection on behavioural traits (Grafen 1984).

Eusociality has inspired a multitude of theories that try to explain its origin and evolution. Some of these theories have been formalized in mathematical terms and some others not. Mathematical formalizations have mainly followed the kin selection and group selection framework (see introduction) (Hamilton 1964*a*; Marshall 2011, 2015). More recent attempts to model the evolution of eusociality claim to rely on population genetic models (Nowak et al. 2010; Fromhage and Kokko 2011; Nonacs 2011; Avila and Fromhage 2015; Olejarz et al. 2015). Although modelling eusociality with population genetics is not entirely novel; Hamilton's original derivation of inclusive fitness is underlain by a population genetic model (Hamilton 1964*a*, 1964*b*). Irrespective of the mathematical formalization, all of these theories have focused only on the selective part of the evolutionary processes, and have ignored the development of the colonies and the worker trait itself. In contrast, conceptual theories of the evolution of eusociality have highlighted proximate causes that lead to the origin of the worker trait (Alexander 1974; West-Eberhard 1987*a*, 1987*b*, 1996; Hunt 2012). Selection- and development-based theories are not mutually exclusive or oppose each other; rather they can naturally complement one another (Uller and Helanterä 2014).

The theory of maternal manipulation postulates that eusociality evolves due to the capacity of mothers to force their offspring to stay in the natal nest (Alexander 1974). If offspring do not evolve the tendency to stay in the nest to help their mother, because such action does not increase their inclusive fitness, the mother, given their influence on the offspring development, can force them to stay and work. In other

words, the theory explains eusociality by postulating that the mother has the upper hand in the conflict between her and her offspring. When comparing kin selection and maternal manipulation, Alexander (1974) himself acknowledges that genetic relatedness is still necessary for selection to favour worker behaviour under maternal manipulation. He argued that maternal manipulation is just a mechanism that favours the origin of the trait, and its future selection. From a kin selection perspective, the fact that the trait determining the behaviour is expressed in the mother, and not the offspring, changes the inclusive fitness calculations. The relatedness component in Hamilton's rule (1964*a*) would stand for the relatedness between the mother -the new actor- and her offspring, rather than between the workers and their siblings (Nonacs 2014). However, assuming a full maternal control of the behavioural phenotype of all her offspring seems biologically unrealistic; especially when dealing with the origin of the worker phenotype. A more reasonable scenario is that the worker phenotype is under control of the worker, and the mother can have some influence in directing the expression of the trait (Uller and Pen 2011). Such type of evolutionary scenario of maternal manipulation has shown to indeed favour the evolution of the worker trait (González-Forero 2015). Moreover, the model exemplifies that kin selection theory is compatible with theories that address the origin and expression of the worker trait. The leading formal theoretical framework that focuses on the effect of natural selection on the evolution of eusociality, kin selection, implicitly assumes that the altruistic or worker trait is subject to phenotypic plasticity (West-Eberhard 1987*b*; Schwander et al. 2010). In a hypothetical scenario where a group of individuals carrying the allele for altruistic behaviour have a life-long interaction, at least one of them should refrain from expressing the altruistic trait, if the trait is to be selected for. This is because altruistic individuals do not reproduce. By refraining from expressing the trait, the non-altruist individual would reproduce, enjoy the benefits of the action of the altruistic partners, and pass the altruistic allele on to the next generation. Thus, the altruist trait must be facultative. The facultative nature of the worker or altruistic trait implies that one of the key questions in the origin of the trait is when is it adaptive to express it (West-Eberhard 1987*b*). In the epigenetical theory of the origins of insect sociality (1987*b*), Mary Jane West-Eberhard argues that the worker trait should be understood not as a new trait, but as the expression of behavioural traits already present in solitary relatives of eusocial species. Solitary insects must time and order the expression of behaviours such as nest construction,

cell construction, oviposition and brood care in the right way to secure the survival and reproduction of their progeny. In the epigenetic scenario, the worker trait in solitary insects emerges when the daughter of a foundress expresses brood care towards the brood of her mother; namely, expressing a pre-existing behaviour in a new social context. The “miss-expression” of this solitary trait could be caused by the presence of a known cue in the new social environment (West-Eberhard 1987a; Linksvayer and Wade 2005; Hunt 2012). For example, a female that stays in the nest of her mother might encounter a brood cell with an egg or larvae already developing. The presence of the developing brood might prime the new hatched female to engage in brood care before her own oviposition has taken place. Furthermore, the activities of females are regulated by hormonal cycles such that oviposition is inhibited by brood care (West-Eberhard 1987a). Hence, by engaging in brood care the female would be postponing reproduction. If such activity is maintained long enough, the female would be a behaviourally sterile worker at her mother’s nest.

Interestingly, Mary Jane West-Eberhard (1987b) stresses that under her epigenetical theory for the origin of the worker trait, kin selection should favour not individuals that carry an allele for altruistic behaviour but rather individuals that express at the correct time of their life cycle brood care behaviour towards their siblings. However, she does not discuss or mention when is it that expressing brood care is adaptive. Instead, she argues that it is possible to disconnect brood care behaviour and oviposition. The answer to the question of when is it adaptive to express brood care towards siblings, rather than offspring, is one of ecology and life-history. The model we present in chapter 3 points to answer the question implicitly posted by the epigenetical theory regarding the origin of the worker trait (West-Eberhard 1987b). We presented a model where individuals of a solitary species produce two broods during their life-cycle. In such a life history set-up, the lifetime of an individual from the first brood overlaps with that of their parents, and with that of their siblings from the second brood, as developing larvae. If individuals from that first brood stay in the natal nest they are in contact with their siblings; thus, they are potentially exposed to the cues that trigger brood care in solitary individuals. Moreover, if the sex determination system is haplodiploidy, and foundresses monogamous, females from the first brood would care for siblings that are more related to themselves than their own offspring, given the female-biased brood (Hamilton 1964a; Trivers and

Hare 1976; Seger 1983; Stubblefield and Charnov 1986). Hence, it is more adaptive for females to express brood care in the natal nest toward their siblings in the second half of a bivoltine life-cycle.

In order to properly time the expression of brood care behaviours, individuals must rely on environmental or social cues. The machinery that responds to these cues can be co-opted from the existent regulation in the solitary bivoltine ancestors (Hunt and Amdam 2005). Species with a solitary bivoltine life cycle express different physiological phenotypes depending on which stage of the cycle individuals are born. Individuals from the first brood reproduce right after hatching. They leave the maternal nest, mate and find a suitable nesting place. In contrast, individuals from the second brood leave the natal nest, mate (under female hibernation life-cycle), and look for a place to overwinter. Thus, they enter a state of metabolic diapause, which is already distinguishable at the larval stage (Shintani 2011). Before overwintering, individuals must store fat reserves and shut down the metabolic pathways involved in ovary development and reproduction. All in all, the metabolic and physiological phenotype of individuals from the two broods is different. In order to tune their metabolism and physiology, individuals must respond to cues from the environment such as temperature, photoperiod and larval nourishment. All these cues can potentially be co-opted for the expression of allomaternal care towards siblings of the second brood. Note that larval nourishment is a signal partly controlled by the foundress; thus, it opens the possibility for maternal manipulation as proposed by Alexander (1974). Further evidence for the homology of the two phenotypes in solitary bivoltine species and the queen and worker caste in eusocial nests is the different life-spans that the phenotypes present. The overwintering phenotype and queens have a much longer lifespan than the first brood phenotype and workers. Thus, the physiological differences between the solitary phenotypes could underlie the lifespan differences between queens and workers.

In the models of chapters 3 and 4, for the sake of simplicity and clarity, we have assumed a simple direct relation between the quantitative value of an allele (h) and the probability of females from the first brood to stay as workers. Hence, we have ignored the mechanisms that allow these females to respond to environmental and social cues. Moreover, we have ignored the potential role that the foundress might

have in triggering the worker behaviour. Thanks to these simplifications we have been able to show in a clear way the effect of a set of preadaptations in the evolution of eusociality (chapter 3). However, there is no reason why the same life-history cannot be used to model the evolutionary dynamics of the signal-response system that underlies the expression of the worker trait. Such a model could include the selective aspects studied in the model presented in this thesis and unveil the developmental aspects of worker behaviour. The same framework we used to study the effect of preadaptations related to the ecology, life-history and genetics of species, could be used to assess the effect of different developmental programs on the evolution of eusociality.

In figure 1, I present a schematic representation of a conceptual theory of the evolution of eusociality including selective aspects highlighted in chapter 3, together with the developmental aspects discussed originally by Mary Jane West-Eberhard (1987*a*, 1987*b*), and elaborated by James Hunt (2012). Figure 1a shows the life cycle of a solitary partially bivoltine population. Mated females (purple) emerge from hibernation and raise a male-biased brood (Fig. 1a, chapter 3). Developing females from the first brood are exposed to environmental factors such as day-length and temperature (red-blue arrow), and to the larval nourishment provided by their mother (purple arrow). These cues and signals allow females to develop into the summer phenotype (pink females) that hatches ready for reproduction and cannot go into diapause; other solitary insects have been shown to respond to these type of cues (Shintani 2011). Both spring and summer females raise a brood that is female biased (chapter 3). The females from this brood develop under different environmental conditions than the summer females, and receive different cues and signals from their mothers. This information is used by the larvae to develop into the phenotype that will postpone reproduction and enter diapause. In a second stage (Fig. 1b), some of the females from the summer brood delay dispersal from the natal nest, and express maternal care toward their siblings from the autumn brood. This behavioural change could be triggered either by environmental changes or changes in the maternal effects (Alexander 1974; Hunt 2012). The standing genetic variation in the genes involved in the signal-response system that determines the developmental path a female will follow would make some females more responsive to the environmental changes. The females that stay and care for their siblings would be raising a brood that is

more related to themselves than their own offspring (Trivers and Hare 1976; Seger 1983; Stubblefield and Charnov 1986). Thus, even if females staying at their natal nest are less efficient at raising siblings than offspring, their behaviour would be favoured by natural selection, and a population with a life-cycle as the one depicted in figure 1b would evolve towards the one depicted in figure 1c. In this life-cycle, the first brood has turned into a worker brood and the second into a reproductive brood. Note, however, that the signal-response system still responds to the environmental influences; hence, individuals can, under certain circumstances, deviate from the worker phenotype. In figure 1d, I depict the same life cycle with the difference that the signal response system only responds to signals from the social environment (mother and sister workers). This further integration of the developmental system and the social environment is likely necessary for the further elaboration and specialization of the caste system seen in advanced eusocial insects (Wheeler 1986). Finally, it's worth noting that a life-cycle like the one presented in figure 1d, could easily make a transition to a 'perennial' colony (one that lives more than one year). The production of the worker brood could be extended in a tropical environment where the seasons are less pronounced, and the environmental cues for producing workers remain in place for longer.

The developmental evolutionary scenario depicted here combines elements of the kin selection models developed in this thesis, and the developmental scenarios hypothesized elsewhere (West-Eberhard 1987*b*, 1996; Hunt and Amdam 2005; Hunt 2012). A mathematical formalization of the scenario presented here requires assuming the genetic machinery underlying the signal-response system that determines the developmental pathways in females. Assumptions about this system can be informed by recent advances in evolutionary developmental genetics of social behaviour (Toth and Robinson 2007), as well as from comparative socio-genomics (Kapheim et al. 2015). I believe that formal modelling of these ideas could take us a long way towards an evolutionary developmental theory of the evolution of eusociality.

Density regulation in the bivoltine model

One of the first objectives of behavioural ecologists interested in social animals was to find ecological factors driving the evolution of cooperatively breeding species. Ecological constraints and life history characteristics have been proposed as main

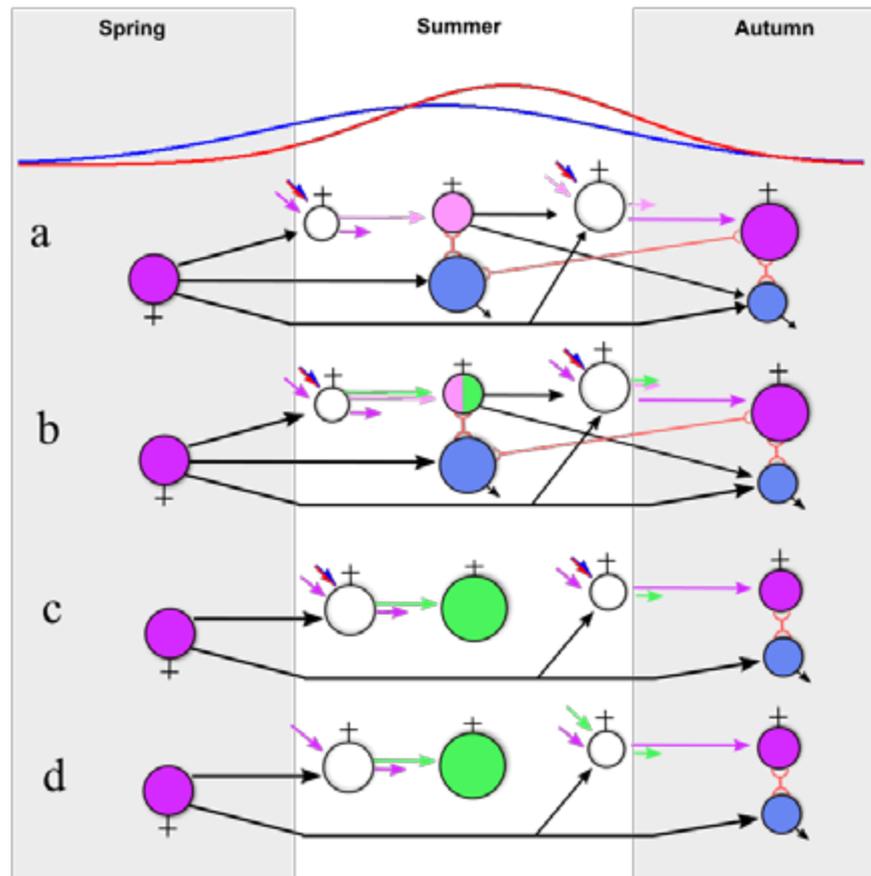


Figure 1. Outline of an evolutionary developmental theory of eusociality. The blue and red curves at the top depict hypothetical environmental changes in two variables throughout one reproductive season. Life cycles a through d depict 4 transitional stages of behavioral and life-history evolution starting in a solitary partially bivoltine life-history (a) to advanced eusociality (d). In (a) individuals breed solitarily and provide maternal care to their offspring. Females (purple) emerge from overwintering in the spring and produce two broods. The first brood is male-biased while the second is female-biased. First brood females (pink) contribute to the autumn brood; thus, they reproduce right after hatching. Autumn brood females (purple) mate and enter into hibernation to withstand the winter. Life-history differences of females from the two broods imply also differences in physiology and metabolism. Differences are caused by different developmental pathways taken at the larval state (blank females). At the larval state, females use environmental cues (red-blue arrows) and social cues from their mothers (pink or purple arrows) to decide which developmental pathway to take. In b the worker phenotype appears (green). Triggered by either environmental changes or maternal cues, some of the first brood females (pink-green) delay dispersal and express maternal care towards their sibling from the second brood. If they do so, they help raise a brood to which they are more related (chapter 3). Thus, natural selection favours developmental plans that trigger allomaternal care (green), leading the population to c, a eusocial univoltine life-history where the first brood is composed of female workers only, and the second one of reproductives. Environmental cues and maternal signals underlie the decision of whether to become a worker or a reproductive. Finally, in d the cues necessary to determine the developmental pathway of females are in control of the colony; either foundresses or workers control the cues to lead larvae in the developmental decision. This opens the possibility to a more elaborate caste system.

factors causing the evolution of cooperative breeding (Emlen 1982; Arnold and Owens 1998). Both of these frameworks stress potential ecological and life-history factors that restrain the breeding opportunities of new offspring. Due to the restricted breeding options individuals might be selected to delay dispersal and help in raising siblings (Pen and Weissing 2000a). Until recently, the lack of breeding opportunities had not been used for explaining the evolution of eusocial insects. That is because the arguments implicitly assume a population with overlapping generations living in a saturated habitat, where there is a shortage of available breeding spots for juveniles. Life histories of social insects typically involve a hibernation period where the breeding spots become available again for newly hatched individuals (Schwarz et al. 2007). A recent model, however, proposes ecological constraints as a potential driver of eusociality (Avila and Fromhage 2015). The authors argue that in a saturated environment with strong density regulation, it will be difficult for newly hatched offspring to find a breeding spot, while their mother already has acquired one; thus, it will be a better strategy to stay in the natal nest and help raise siblings.

The model presented by Avila and Fromhage (2015) does not mimic the life history of taxa with primitively social species; thus, its applicability to understand the evolution of eusociality is limited. However, the model does show that the lack of breeding opportunities can have an important impact on the evolution of eusociality. In the model presented in chapters 2 and 3, we obviously assume density regulation acting in the bivoltine population (see supplementary material of the corresponding chapters). We assume that density regulation occurs during the winter season: only a fraction of the females from the second brood actually make it to the spring and found nests. Several mechanisms of density regulation are in line with this assumption. For instance, density regulation could occur through the death of a fraction of females that cannot stand the low temperatures; or successful overwintering could require finding a place with certain conditions, and these places might be limited in a given habitat. Density regulation at the overwintering stage does not limit the breeding opportunities of the potential workers from the first brood because it acts on the second brood. This is in line with our results (chapter 2) showing that it is the increased relatedness, driven by haplodiploidy and sex ratio biases, the one that favours workers that are less efficient at raising siblings than offspring. Nevertheless, one can think of alternative density regulation mechanisms that do limit the breeding

opportunities of potential workers; resulting in the effect described by Avila and Fromhage (2015).

Density regulation driven by a constant number of breeding spots available for the population could limit the breeding opportunities for potential workers, favouring the evolution of eusociality. In the models presented in chapters 2 and 3, we assume that females from the first brood decide whether to stay and work in their natal nest, or seek their own breeding opportunities. If they decide to seek their own reproduction, they mate and find a suitable nest. This assumption, in a way, is a worst case scenario for the evolution of eusociality. The cost paid by a female that decides to stay and work is not diminished by low probabilities of finding a suitable nest. If we were to assume that density regulation is enforced by strict limit in the number of suitable nests, we would have to weigh the reproductive potential of first brood females by the per capita probability of finding a suitable nest. Thus, the selection differential of helping behaviour (equation 45 in the supplementary material of chapter 2) would have to be changed to

$$\left. \frac{\partial W_h}{\partial h} \right|_{h=h^*} = F_3 \left[-\tilde{a} (\tilde{z}_2 r_{\text{dau}} v_{f2}^* + z_2 r_{\text{son}} v_{m2}^*) + B (\tilde{z}_2 r_{\text{sis}} v_{f2}^* + z_2 r_{\text{bro}} v_{m2}^*) \right] \quad (1)$$

where γ is the per capita probability of first brood females to find an available breeding place, and varies between 0 and 1. The larger γ is the more difficult it will be the evolution of the helping trait. γ can be easily derived from the assumption on density regulation. If density regulation is driven by a constant number of breeding spots throughout the season, gamma is given by the ratio of breeding spots freed by mortality and the number of first brood breeding females, technically

$$\gamma = \frac{1 - S_f}{F_1 \tilde{z}_1 h} \quad (2)$$

Equations (1) and (2) together show that under this new mechanism of density regulation the effect of natural selection on the helping trait is influenced by specific life history quantities. High female survival, as well as a larger number of females from the first brood, reduces the chances of finding a breeding spot, favouring the evolution of the helping trait. Note that the results obtained in chapter 2 on sex ratio evolution indicate that natural selection would lead foundresses to produce

fewer females in the first brood, reducing the positive effect of density regulation. Also noticeable, the population helping tendency reduces the strength of the density regulation process. Thus, even if density regulation favours the initial invasion of the worker trait, this effect might be ephemeral along the evolutionary process. All in all, the preliminary analysis shown here evidences the need to formally account for density regulation; and more importantly, it is necessary to inform the density regulation assumption by the natural history of social animals. The relevance of the arguments laid here will most likely depend on the ecological situation in which eusociality evolved. This is also an open question.

Understanding the diversity of eusocial insects

The haplodiploidy hypothesis is the first theoretically derived insight that proposed an explanation for the phylogenetic distribution of eusociality (Hamilton 1964a, 1964b). Hamilton argued that the relatedness asymmetry caused by the sex determination system made eusociality more likely to evolve in haplodiploid systems (see Fig. 4 in the introduction of this thesis). This argument stems from his general derivation of inclusive theory, and the calculation of relatedness coefficients between females of a haplodiploid colony, but without a specific model. Despite Hamilton's lack of a formal model checking the verbal arguments of the haplodiploidy hypothesis, he certainly developed the appropriate methods for making this formalization. Over the years many models have been developed formalizing the idea of haplodiploidy favouring eusociality, and clarifying when this can be the case (Trivers and Hare 1976; Iwasa 1981; Seger 1983; Stubblefield and Charnov 1986; Fromhage and Kokko 2011; Gardner et al. 2012; Johnstone et al. 2012; Alpedrinha et al. 2013, 2014; Rautiala et al. 2014; Avila and Fromhage 2015). All this theoretical work has not reached an agreement on whether generally eusociality is favoured by haplodiploidy, but it has certainly improved our understanding of the effects of haplodiploidy on particular ecological and life history conditions.

A logical step, given the theoretical knowledge acquired in the last years, would be to match the models with empirical data. However, progress in that respect seems meagre compared to the one on the theoretical understanding. A simple statistical analysis of the number of families that have haplodiploidy and eusociality shows eusociality to be skewed towards families with haplodiploid sex determination (Crozier 2008).

However, this simple analysis does not correct for potential phylogenetic biases, or other preadaptations that are also present in families with haplodiploidy. Thus, evidence is not definitive on a statistical bias towards haplodiploids in the distribution of eusociality. A more elaborate statistical analysis indicates that monogamy most likely preceded every event of the evolution of eusociality (Hughes et al. 2008). Monogamy is a trait that many models have predicted to favour the evolution of eusociality (Boomsma 2009; Fromhage and Kokko 2011; Gardner et al. 2012; Avila and Fromhage 2015; Davies and Gardner 2016). Although Hughes et al.'s (2008) analysis is a commendable effort to test predictions derived from theory, it focuses on only one trait, and it derives the prediction from a general kin selection argument rather than from a specific model of the evolution of eusociality.

A more complete explanation of eusociality requires an understanding of ecological, life history, genetic and developmental aspects influencing its evolution; furthermore, it requires a mutual feedback between empirical studies of social animals and theoretical studies unveiling causal links. Thus, model assumptions need to be substantiated by the natural history of social animals; and models must provide testable predictions. I believe the model presented in chapter 3 to be a stepping stone in that direction. First, the life history structures we modelled were inspired by primitively social insects. Secondly, the parameters that crucially define the behaviour of the model have clear life history interpretations. Hence, model predictions can be potentially matched with statistical analysis of the interspecific variation in the parameter values and life history characteristics. It is worth mentioning that our model uses the same life histories as the model developed by Seger (1983), and that sex ratio predictions from his model could not be validated with empirical data (Brockmann and Grafen 1992). Brockmann and Grafen were mainly trying to find male overlap and right kind of sex ratio biases in one bivoltine species. However, our model clearly shows that if females have the capacity to produce different sex ratios in the two broods, the coevolution of sex ratio and social behaviour would erase any traces of male overlap. Thus, rather than looking for one example of a species with the right biases, statistical analysis of interspecific variation could try to find correlations between key life history characteristics (Kocher and Paxton 2014); for instance, female hibernation, and eusociality. For that specific example of female hibernation, there is already some evidence from paper wasps in line with our

predictions (Hunt 1999). Another key feature that our model indirectly points at is the length of the reproductive season. If, as our model (chapter 3) and developmental data (Hunt and Amdam 2005) indicate, bivoltinism is a preadaptation for eusociality, then ecological traits that favour a breeding season long enough to have two broods should correlate with social behaviour. A recent meta-analysis shows precisely that prediction to hold in a latitudinal gradient (Kocher et al. 2014). These examples show the potential of combining comparative methods and theoretical models to illuminate the mechanisms behind social evolution.

The evolution of altruism has been the main focus of models attempting to understand the evolution of eusociality. Altruism is indeed the cornerstone of eusociality. However, individuals in eusocial societies face many other social conflicts, and their existence and resolution define some of the interspecific variation in eusocial species. Traditionally, models addressing the evolutionary consequences of these conflicts treated them separately. Recently, coevolutionary models of the traits underlying the conflict have shown to add considerable insights to our understanding of eusocial insects (Wenseleers et al. 2013). In chapter 3 of this thesis we used the same approach by extending the bivoltine model of chapter 2 to include the sex allocation conflict between queens and workers. The model showed the evolution of societies with different levels of altruism, sex allocation patterns and life history structures. The evolved life cycles match some of the species found in primitively social insects (see references chapter 3); thus, potentially contributing to understand interspecific variation in social species. As argued above, a statistical analysis of the interspecific variation in social structures, queen and workers sex allocation strategies could validate the explanation provided by our models.

Interspecific variation in social behaviour in the different families of primitively social insects arises not only through the transition from solitariness to eusociality, but also due to the reverse transition in some species (Danforth et al. 2003; Brady et al. 2006). Despite the prevalence of reversals to solitary life, there is no formal evolutionary explanation of why some species lose the worker trait. One potential explanation is that social life comes along with new selective pressures and that some species are not equipped to deal with those pressures. In which case, solitary behaviour might invade, leading to a reversal in social behaviour. For instance,

social life will probably come along with higher rates of pathogen and parasitoids transmission, due to the constant contact between individuals of a colony (Cremer et al. 2007). Some species might have evolved better strategies than others to deal with the new immunological pressures. Individual traits that facilitate social immunity will allow colonies to thrive despite the challenges of higher pathogenic pressure. In chapter 2, we presented data adding to the mounting evidence that extended brood care is a preadaptation to eusociality (Plateaux-Quénu 2008). There is, however, no clear mechanistic explanation of how extended brood care facilitates eusociality. Extended brood care could reduce the pathogenic pressure of a newly social species. Modelling studies could test verbal arguments and provide some prediction of when we would expect reversals to solitary life due to higher pathogenic pressure. More generally, a complete picture of social insects requires a better understanding of why some species revert back to solitary life.

Concluding remarks

At the beginning of these afterthoughts, I described what a major evolutionary transition is, and why eusociality was chosen to be one of them. Maynard Smith and Szathmáry stressed in their seminal book that a key question that must be answered to understand all major transitions is: why did the action of natural selection at the lower level not disrupt the formation of the higher level? In this thesis we presented some models showing how a certain set of conditions (preadaptations), which evolved before eusociality, align the fitness interests of workers with that of their colony. The alignment of fitness interests between the two levels of organization explains why natural selection favoured the formation of a primitive new level organization, the eusocial colony. A second element stressed by Maynard Smith and Szathmáry is that of new path of information transmission and storage. I argue this aspect of information transfer in the major transition to eusociality has been mostly ignored by formal evolutionary models of eusociality, including the ones presented in this thesis. In contrast, the information aspect has been salient in developmental theories of the origin of the worker trait (West-Eberhard 1987*a*, 1987*b*, 1996; Hunt 2012). In this closing section I discussed how the insights obtained from our modelling efforts can be part of a more integrative theory of the evolution of eusociality. Particularly, I discussed how the bivoltine model can be a unifying life-history aspect between evolutionary theories of eusociality and developmental theories of the origin of the

worker trait. Furthermore, I argue that the models presented here can be used to provide predictions that are subject to be tested with comparative methods; deepening the link between theoretical models and natural history of social insects is necessary for advancing in our understanding of the major transition to eusociality.